

[COMMUNICATION]

A Centrolenid-Like Anuran Larva from Southeast AsiaROBERT F. INGER and RICHARD J. WASSERSUG¹*Field Museum of Natural History, Roosevelt Road at Lake Shore Drive,
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ABSTRACT—Vermiform tadpoles of the treefrog family, Centrolenidae, live buried in leaf litter on the margins of streams in the New World. These tadpoles have, among other features, long tails with reduced fins, small, subcutaneous eyes and highly vascularized, nearly pigmentless skin. We describe here the first tadpole from Southeast Asia with this morphology. The tadpole was collected in a microhabitat similar to the one in which centrolenid larvae have been found. Except for the fact that the Bornean larva has more denticle rows, the tadpoles are virtually identical in external morphology. The Bornean tadpole probably belongs to either a ranid or rhacophorid genus but, since no metamorphic individuals with adult diagnostic features have been found, the taxonomic assignment is uncertain.

INTRODUCTION

The Centrolenidae is a well-defined family of arboreal frogs restricted to Central and South America. Tadpoles have been described for less than a fifth of the 65 known species, yet those described are sufficiently similar to one another in ecology and morphology, while different enough from other known larvae to characterize the family [1].

Centrolenid tadpoles are found only in association with streams. Those collected in the field have been found burrowed into decaying vegetation at the edge of the water, not exposed to the current. These tadpoles are characterized by having long tails ($\geq 2 \times$ the head-body length) with reduced dorsal and ventral fins, depressed or cylindrical bodies, small dorsal eyes covered with skin, and

reduced pigmentation. All of these features seem directly related to their fossorial way of life.

In this paper, we describe a centrolenid-like tadpole from Borneo. At present we can identify the larva only to suborder. Subtle oral features distinguish this larva from true centrolenid larvae; otherwise the convergence in microhabitat use and overall morphology is among the most precise that we know of for amphibian larvae.

RESULTS

Four specimens have been collected (Table 1) from two localities (Danum Valley Field Centre, Lahad Datu District, Sabah and Nanga Takalit, Kapit District, Seventh Division, Sarawak) and deposited in the Field Museum of Natural History (FMNH). The following description is based on the largest specimen collected so far, a stage 31 of Gosner [2] individual.

The general body form is ovoidal, strongly depressed. The eyes are dorsal, extremely small, below the skin and far posterior from the tip of the snout. The eye-snout distance is one-third the head-body length. The pupils are directed obliquely dorsolateral. Eye diameter is 8% of head-body length; interorbital distance is 60% of the internarial distance. The nostrils are small ($< 1\%$ of head-body length), lack an elevated rim, and are exceptionally far forward. They are just dorsal to the lateral edge of the snout, above the corner of the mouth, at 11% of distance from snout back along the head-body.

The oral disc is ventral, subterminal. Its width is $2/3$ the maximum width of the body. The marginal

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TABLE 1. Measurements¹ and denticle counts of fossorial stream-associated tadpoles from Borneo

Specimen(s)	FMNH #31452	FMNH #221024
Locality	Danum	N. Takalit
No. individuals	1	3
Stages ²	31	25
Head-body length	10.0	5.4-6.5
Head-body depth	5.2	3.3-4.0
Head-body depth	3.6	2.1-2.3
Eye diameter	0.8	0.3
Eye-snout	2.8	1.7-2.2
Nostril-snout	1.1	0.7(1)
Interorbital	1.4	1.1-1.2
Internarial	2.3	—
Snout-spiracle	7.1	4.5-4.8
Tail length	22.5	10.4-13.0
Tail depth	4.7	2.7-3.3
Denticles ³		
-upper	I:1-1	I:1-1
-lower	1-1:VIII	1-1:VIII

¹ Measurements made with ocular micrometer at 12×, given in mm; definitions of dimensions as in Inger and Frogner [15].

² According to Gosner [2].

³ Follows system used in Inger [3].

papillae are in a single row with a narrow median gap along the posterior free edge of the disc. The papillae are of moderate size. Papillae are absent along the anterodorsal edge of the disc, but are clustered on a small outwardly directed flap at the lateral corners of the mouth. A distinct notch separates these flaps from the ventral portion of the disc. The papillae on the lateral flaps are the largest and are in two rows, seven to nine papillae in an outer row and two to four in an inner row.

The dental formula, following the system of Inger [3], is I:1-1/1-1:VIII. The denticles in the ventral rows decrease in size from the inner-most to outer-most rows and the four outer-most rows are distinctly shorter than the inner ones. The denticles are dense, spatulate and range from black (large) to brown (small) in color. They all curve toward the mouth. In microscopic detail, they most closely resemble the denticles illustrated for *Rana chalconota* and *Rana signata* in Inger [3].

The upper beak is a wide, gentle arch. The margin is finely serrated. The marginal serrations are of uniform size, smaller than the denticles, and

darkly pigmented. The lower beak is V-shaped, with an angle of 100° between the arms. The pigmented margin of the lower beak is slightly more extensive than that of the upper beak; its serrations are coarser than those of the upper beak, but still finer than the neighboring denticles.

The spiracle is sinistral, midway up the side of the body and far posterior (i.e., 70% of distance

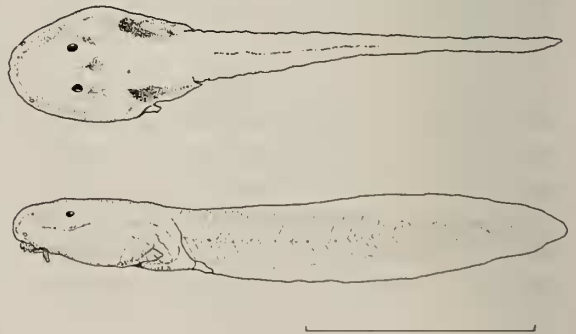


FIG. 1. Dorsal (above) and lateral (below) views of the fossorial ranoid tadpole described in this report. The illustration is of a stage 25 specimen (FMNH #221024) See Table 1. Scale line=5.0 mm.

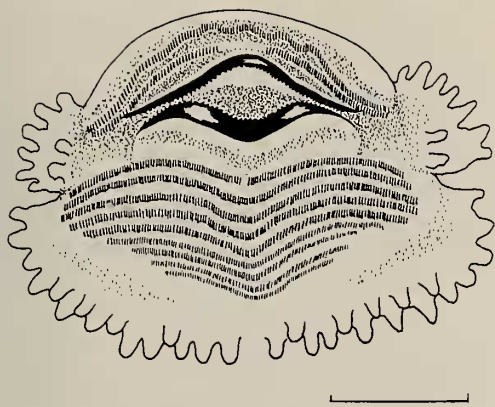


FIG. 2. Oral disc of the tadpole illustrated in Fig. 1. Scale line=0.5 mm.

from the snout tip to end of body). The spiracle has a short, free, terminal tube. The width of the spiracular opening is slightly greater than the diameter of the eye.

The anal tube is median and long.

The tail is long and slender, $2 \frac{1}{4}$ times the head-body length (Table 1). The tail tip is broadly rounded. The fin margins are very weakly convex. The maximum depth of the tail is at approximately $\frac{3}{5}$ of tail length. Both the dorsal and ventral fins are shallow. The dorsal fin begins on the tail just above the end of the anal tube. The ventral fin begins immediately behind the body proper and is slightly deeper than the dorsal fin in the proximal $\frac{1}{3}$ of the tail. The caudal musculature is deeper than either fin in the proximal $\frac{2}{3}$ of the tail.

The head-body of the preserved tadpole is pigmentless. The skin on the body has a shiny appearance. The skin overlying the caudal musculature has a faint, brownish reticulum. This pigment pattern extends up on to the dorsal fin near the base of the tail.

Neuromasts are present but not easily observed or counted. They are singular, not organized into stitches. Approximately 20 neuromasts are present in both the infraorbital and supraorbital rows on each side of the head.

The posterior $\frac{2}{3}$ of the intestines, along with a portion of the pancreas, are visible through the ventral body wall. We counted five coils of intestine from the center of the gut to the caudal edge of the body cavity.

Because the internal oral features of this tadpole are so similar to those of *Centrolenella fleischmani* [4], only features that differ from *C. fleischmani* are described here. Terminology follows Wassersug [4].

The medial pair of infralabial papillae are smaller. The lateral pair of infralabial papillae are larger with finger-like projections. There are four buccal floor arena papillae per side. The prenarial arena has a small, median knob anteriorly and a larger transverse ridge posterior to it. The long, longitudinally oriented, internal narial depression that characterizes *C. fleischmani* is absent. The median ridge is smaller and more posterior. The postnarial papillae are much larger. They have rounded apices and project anteromedially over the medial half of the internal nares. Additional flap-like papillae of the anterior buccal roof are absent. The dorsal velum is not continuous across the midline. The glottis is smaller and not patent.

Qualitatively, the structure in the pharynx of this specimen looked indistinguishable from those of *C. fleischmani*. Secretory ridges are present on the branchial food traps. Because of the small size of the specimen, no attempt was made to count gill filter rows.

The lungs at stage 31 are large, as long as the body cavity and flattened, indicating that they were not inflated in life. The skin is heavily vascularized.

Fine, heterogeneous particulate matter fills the alimentary tract. No macroscopic fragments of arthropods or plants are present. Some small mineral grains are visible, but most of the contents are unidentifiable organic debris.

Taxonomic considerations

The most mature tadpole collected so far is still too young to reveal any adult diagnostic characters. Adult frogs in the neighborhoods where these fossorial tadpoles were collected comprise pelobatids, bufonids, ranids, rhacophorids, and microhylids [5, 6]. The presence of denticles, a sinistral spiracle and perforated nares immediately exclude the tadpole from the Microhylidae [7]. The oral disc papillation, denticle row counts and denticle morphology are unlike any Bornean bufonids or pelobatids. The tadpole is by elimina-

tion tentatively classified as ranoid, either Ranidae or Rhacophoridae. Further assignment to family or genus is not possible at this time.

DISCUSSION

Our Bornean tadpoles were collected in deep leaf litter within but near edges of clear streams in lowland primary rain forest. The three in stage 25 were taken with larvae of two bufonids (*Ansonia leptopus* and *Pedostibes hosei*), and a pelobatid (*Leptobrachium montanum*). The stage 31 tadpole was found with larvae of *Rana signata*. All of these, except for the larval *Leptobrachium*, are commonly found in drifts of dead leaves [6].

Although Duellman and Trueb [1] claim that centrolenid tadpoles "develop in gravel or detritus in flowing water", to the best of our knowledge free-living centrolenid larvae avoid both flowing water and gravelly substrates. Rather they are found within the "accumulation of leaves, sticks and mud" [8] or occasionally even in the humus of a stream bank above the waterline [9] and out of the current. The common microhabitat of centrolenid larvae closely resembles the microhabitat where our unusual Bornean tadpoles were collected.

Except for the denticle formula and narial position, our Bornean tadpoles are externally identical to those of many centrolenid species [10]. The body profile, spiracle position, tail length, fin shape, and overall size and coloration are the same. So are the small nostrils and the small, dorsally positioned, sub-cutaneous eyes. The most conspicuous feature that distinguishes the Bornean tadpole from centrolenid larvae are the supernumerary, ventral denticle rows. Centrolenids all have two or fewer upper rows and three or fewer lower rows.

Internally our tadpole can be distinguished from *C. fleischmanni* by a variety of anatomical features, primarily anteriorly near the orifice of the mouth and the internal nares. These may be little more than internal reflections of differences in external oral morphology and narial position (slightly more anterior in the Bornean species). In key features, which reflect the filter-feeding capacity of the tadpoles—such as the pattern of papillae

on the buccal floor and roof, the shape of the ventral velum, filter plates, and gill filters—the tadpoles are indistinguishable.

Virtually all of the features that distinguish both the Bornean species and centrolenid tadpoles from typical ranoid and bufonid larvae can be understood as adaptations for a fossorial rather than either pelagic or demersal existence [9, 11, 12]. Not all fossorial tadpoles are associated with stream bank leaf litter, but all have cylindrical or depressed bodies and long tails with reduced fins. All have small dorsally located eyes and reduced pigmentation. Several arboreal tadpoles from a variety of anuran families fit this description [13]. The Bornean species is exceptional among all fossorial tadpoles in its high number of ventral denticle rows. We have no functional explanation for this distinctive feature. Another noteworthy feature in the Bornean species is the uninflated lung. This tadpole does not breathe air like certain arboreal and semi-terrestrial "fossorial" tadpoles [10, 13]. Villa [9, 14] suggested that centrolenid tadpoles, which are often reddish in life, appear so because of perfusion of skin for cutaneous respiration. Although the Bornean tadpoles were not particularly reddish in life, the extensive vascularization of their skin supports the idea that they rely heavily on cutaneous respiration.

As a final note, although we have formally described a single form of centrolenid-like tadpole from Southeast Asia, we suspect that other Old World species may have tadpoles of this type.

All other tadpoles collected with our fossorial form have been collected frequently and in large numbers in Bornean stream leaf litter [6]. The rarity of the fossorial form suggests that it may have been displaced into a slightly more aquatic situation than where it normally resides. Truly fossorial tadpoles are notoriously difficult to collect [9], as evidenced by the fact that larvae are known for less than 20% of centrolenid species in contrast to 25–30% for remaining anurans. Among tropical faunas the tadpoles of Borneo are well known [3], but even there tadpoles are known for only about 50% of the species.

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REFERENCES

- 1 Duellman, W. E. and Trueb, L. (1986) *Biology of Amphibians*. McGraw Hill Book Company, New York.
- 2 Gosner, K. L. (1960) *Herpetologica*, **16**: 183–190.
- 3 Inger, R. F. (1985) *Fieldiana: Zool.*, New Series, **26**: 1–89.
- 4 Wassersug, R. J. (1980) *Univ. Kansas Mus. Nat. Hist. Miscellaneous Publ.*, **68**: 1–146.
- 5 Inger, R. F. (1966) *Fieldiana: Zool.*, **52**: 1–402.
- 6 Inger, R. F. Voris, H. K., and Frogner, K. J. (1986) *J. Tropical Ecol.*, **2**: 193–205.
- 7 Wassersug, R. J. (1989) *Fortschritte der Zool.* (In press)
- 8 Heyer, W. R. (1985) *Papeis Avulsos de Zoologia*, **36**: 1–21.
- 9 Villa, J. and Valerio, C. E. (1982) *Brenesia*, **19/20**: 1–16.
- 10 Altig, R. and Johnston, G. F. (1986) *Smithsonian Herp. Information Service*, **67**: 1–75.
- 11 Wassersug, R. J. and Heyer, W.R. (1983) *Canad. J. Zool.*, **61**: 761–769.
- 12 Wassersug, R. J. and Pyburn, W. F. (1987) *Zool. J. Linnean Soc.*, **91**: 137–169.
- 13 Lannoo, M. J., Townsend, D. S. and Wassersug, R. J. (1987) *Fieldiana: Zool.*, New Series, **38**: 1–31.
- 14 Villa, J. (1984) *Milwaukee Publ. Mus. Contrib. Bio. Geol.*, **55**: 1–50.
- 15 Inger, R. F. and Frogner, K. J. (1980) *Sarawak Mus. J.*, **27**: 311–324.